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An enigmatic *Ephedra*-like fossil lacking micropylar tube from the Lower Cretaceous Yixian Formation of Liaoning, China

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Abstract

Angiosperms and gymnosperms are two well-separated groups in seed plants according to the current understanding. The huge gap between these two groups constitutes a serious threat against the Darwinism, which expects a continuous transitional series between them. The Lower Cretaceous Yixian Formation of Liaoning, China is famous for its megafossil angiosperms, including some early angiosperms and putative gnetalean plants. Here we document another *Ephedra*-like fossil plant, *Pseudoephedra* n. gen. n. sp., from the Yixian Formation on the basis of light microscopic (LM) and scanning electron microscopic (SEM) observations. Although its general morphology demonstrates a great resemblance to *Ephedra*, the expected micropylar tube characteristic of *Ephedra* is missing in *Pseudoephedra*. Instead a solid projection is seen on the top of the female parts. Such a puzzling character combination makes *Pseudoephedra* perplexing in seed plant phylogeny. If put in Ephedraceae (Gnetales), *Pseudoephedra* would destroy the only synapomorphy (micropylar tube) of the BEG clade. If put in angiosperms, *Pseudoephedra* would bridge the formerly huge gap between gymnosperms and angiosperms. Apparently, further investigation is needed to clarify the uncertain position of *Pseudoephedra*.

Keywords: Angiosperms; Micropylar tube; Style; Gnetales; China; Early Cretaceous

1. Introduction

The relationship between angiosperms and gymnosperms have been intensively investigated for a long time and much progress has been made in this field recently (Duan, 1998; Sun et al., 1998, 2002; Leng and Friis, 2003, 2006; Ji et al., 2004; Doyle, 2008; Wang and Zheng, 2009; Wang, 2010; Wang and Han, 2011; Doyle, 2012; Wang and Zheng, 2012; Han et al., 2013). The megafossil angiosperms from the Yixian Formation (Lower Cretaceous) have fueled various discussions and evolutionary hypotheses. According to Darwinism, a gradual transition is expected between gymnosperms and angiosperms. However, the assumed intermediate taxon in-between is never found in the fossil record hitherto. Here we report a new fossil plant, *Pseudoephedra paradoxa* n. gen. n. sp. from the Yixian Formation of Liaoning, China. Although resembling *Ephedra* in general morphology, *Pseudoephedra* distinguishes itself from *Ephedra* by a solid apical projection. This minute difference from *Ephedra* makes its placement a headache for plant systematists. Putting it in gymnosperms (Ephedraceae) would destroy the only synapomorphy of BEG group and make angiospermy as if present in Ephedraceae. Putting it in angiosperms would imply that some angiosperms may have general morphology hard to distinguish from Ephedraceae. Apparently, this combination of characters demands a rethinking about criteria used in plant taxonomic practice.

2. Materials and methods

The specimen studied here was collected from the outcrop of the Yixian Formation near Dawangzhangzi, Lingyuan, Liaoning, China (41.1603°N, 119.2680°E, Fig. 1). *Archaefructus* (Sun et al., 2002; Ji et al., 2004) and *Sinocarpus* (Leng and Friis, 2003, 2006) have been found from the same locality. The age

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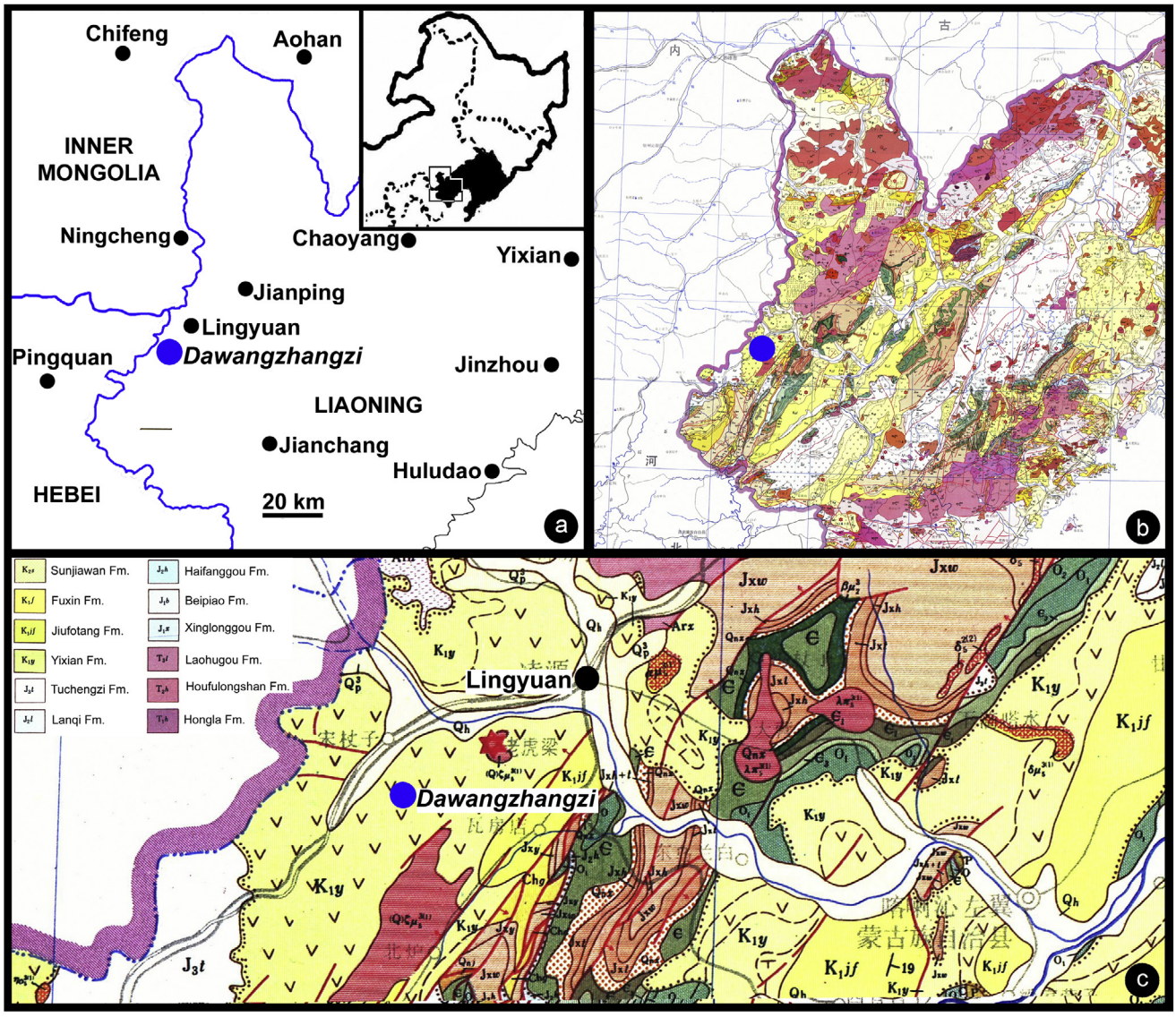

Fig. 1. The geography and geology of the type locality of *Pseudoephedra paradoxa* n. gen. n. sp. (a) The upper right inset shows northeastern China, the black area within is Liaoning Province, and the outlined area is shown in detail in the main map; the black dots are the major cities in the region, and the blue dot is the type locality, Dawangzhangzi Village, Lingyuan City, Liaoning Province, China. (b) Geological map of western Liaoning; note the position of the fossil locality (blue dot); reproduced and modified from attached map 1 of Liaoning Provincial Agency of Geology and Mineral Resources (1989). (c) Geological map of the region near the fossil locality (blue dot), enlarged from (b); K_{1y} = Early Cretaceous Yixian Formation.

of 122–125 Ma (the Barremian or Aptian, Early Cretaceous) is widely accepted for the Yixian Formation (Swisher et al., 1998; Leng and Friis, 2003; Dilcher et al., 2007). The specimen of *Pseudoephedra* n. gen. included two facing parts. The general morphology of the specimen was photographed with a Panasonic DMC-LX5 digital camera. The details of the specimen were observed and photographed using a Nikon SMZ1500 stereomicroscope with a digital camera. Replicas made for the specimen in Fig. 2a were cleaned with 40% hydrofluoric acid, coated with gold, and observed using a Leo 1530 VP scanning electron microscope (SEM) at the Nanjing Institute of Geology and Palaeontology, Nanjing, China. All images were organized together using Photoshop 7.0 for publication.

3. Results

Class, Order, Family *Incertae Sedis*
Pseudoephedra n. gen.

Generic diagnosis: Bracts oppositely arranged along the main axis with obvious joints and internodes. Female parts axillary, more or less pedicellate, surrounded by narrow elongate scales, including a central unit and two surrounding envelopes. Central unit including a proximal oval body and an apical projection. Oval body locular, surrounded by a thin wall. An apical projection solid, long, exserted, with a truncated tip.

Type species: *Pseudoephedra paradoxa* n. gen. n. sp.

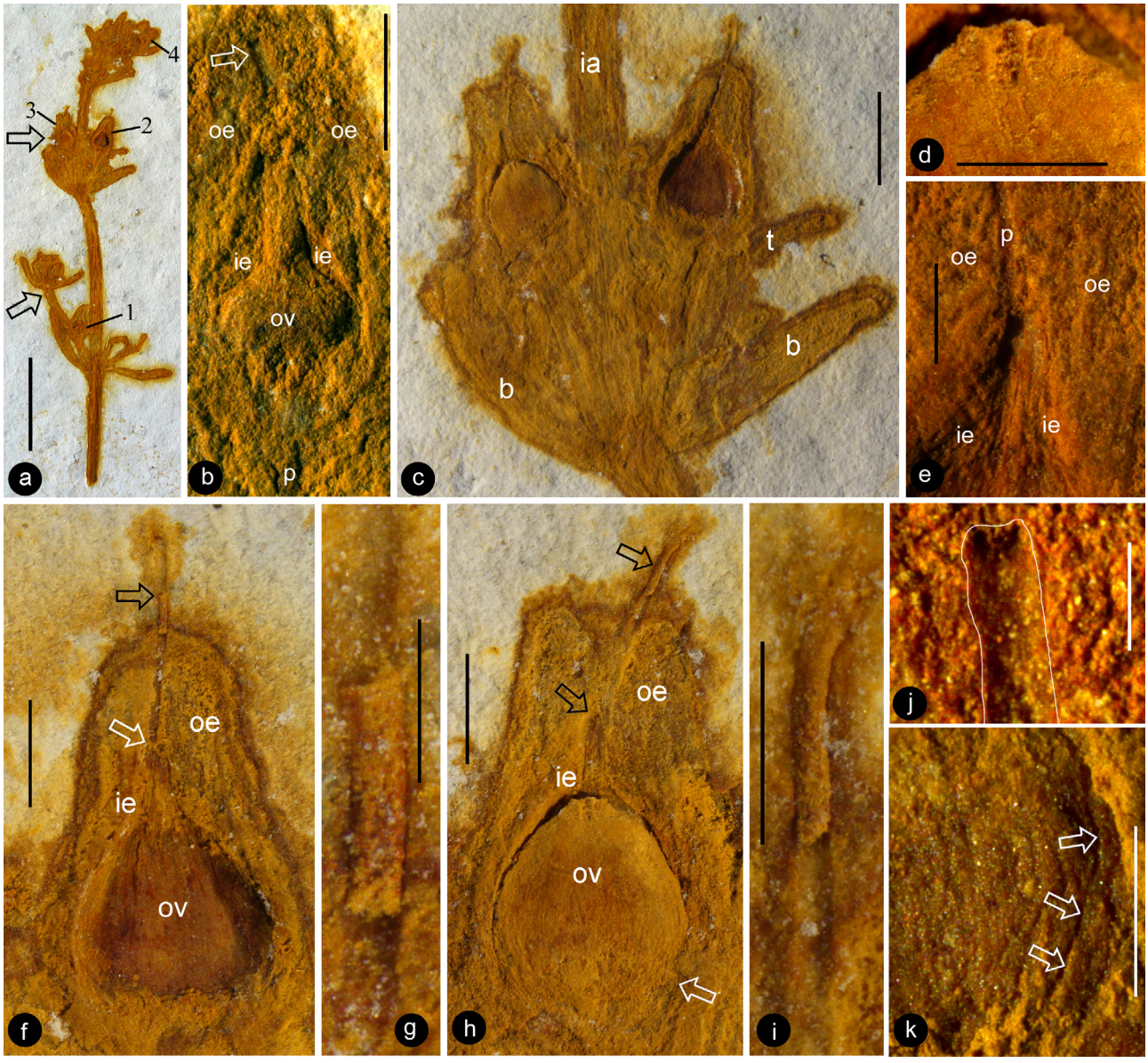

Fig. 2. *Pseudoephedra paradoxa* n. gen. n. sp. and its details. Stereomicroscopy. (a) General view of the fossil with straight axis with oppositely arranged appendages; holotype, NOCC201204261301; scale bar = 1 cm. (b) Female part 4 in (a) showing its pedicel (p), oval body (ov), inner envelope (ie), outer envelope (oe), and apical projection (arrow); scale bar = 1 mm. (c) Two female parts in axils of bracts (b) oppositely arranged along the axis (ia), enlarged from the region marked by the upper black arrow in (a); note the lanceolate scales (t) subtending the envelopes; scale bar = 2 mm. (d) Tip of the solid oval body, enlarged from (h); scale bar = 0.5 mm. (e) Outer and inner envelopes (oe, ie) surrounding the central unit and its apical projection (p); from the counterpart of female part 3 in (a), refer to Fig. 4f; scale bar = 0.5 mm. (f) Female part 2 in (a) broken along its center, showing the inner envelope (ie) and outer envelope (oe) surrounding the oval body (ov) and its apical projection (arrows); note the terminus of the inner envelope (white arrow); scale bar = 1 mm. (g) Detailed view of the apical projection in (f); note the solid cylindrical apical projection either leaves a groove on the sediment (to the top and bottom) or rises as a cylinder above the sediment surface (the middle); scale bar = 0.25 mm. (h) Female part 3 in (a) broken along its center, showing the inner envelope (ie) and outer envelope (oe) surrounding the oval body (ov) and its apical projection (upper black arrow); note the bulging central unit inside the inner envelope and the terminus (lower black arrow) of the inner envelope; scale bar = 1 mm. (i) Detailed view of the three dimensionally preserved apical projection in (h); note that the solid cylindrical apical projection either leaves a groove on the sediment (to the bottom) or rises as a cylinder above the sediment surface (to the top); scale bar = 0.25 mm. (j) A groove in the sediment left by the apical projection of female part in (b); note the truncated terminus and outline (white line) of the apical projection; light from left; scale bar = 0.1 mm. (k) The internal view of oval body portion marked by white arrow in (h) after breaking, showing the inner surface (arrows) of the thin wall around the oval body; scale bar = 0.5 mm.

Etymology: *Pseudo-* for fake in Latin; *-ephedra* for the genus *Ephedra* in Gnetales.

Horizon: The Yixian Formation, Barremian–Aptian, Lower Cretaceous (122–125 Ma).

Locality: Dawangzhangzi Village, Lingyuan City, Liaoning Province, China.

Remarks: *Chengia* and *Siphonospermum* are two fossil genera related to Gnetales from the Lower Cretaceous Yixian Formation of Liaoning, China (Rydin and Friis, 2010; Yang et al., 2013). Both taxa are similar to *Pseudoephedra* in term of axillary female parts subtended by oppositely arranged bracts, apical projection, obvious joints and internodes (Rydin and

Friis, 2010; Yang et al., 2013). In addition, *Siphonospermum* is similar to *Pseudoephedra* in term of two envelopes surrounding the apical projection, elongated pedicel of female part, and elongated apical projection, all of which are much longer and obvious in *Siphonospermum* than in *Pseudoephedra* (Rydin and Friis, 2010). However, *Siphonospermum* is compared to *Gnetum-Welwitschia* clade (Rydin and Friis, 2010) whereas *Pseudoephedra* here demonstrates more resemblance to *Ephedra.* Although both *Chengia* and *Siphonospermum* resemble Gnetales in multiple characters, both publications suffer from lack of detailed information about their apical projections, being tubular or solid. This lack of key information prevents us from further comparing them with *Pseudoephedra*. Given that proving the existence of micropylar tube in fossils is not a mission impossible (Wang and Zheng, 2010; Rothwell and Stockey, 2013), a comparison among *Pseudoephedra*, *Chengia*, and *Siphononspermum* is premature before more detailed information of *Chengia* and *Siphononspermum* is available.

Pseudoephedra paradoxa n. gen. n. sp.
(Figs. 2–4)

Specific diagnosis: Plant part 51 mm long, 17 mm wide. Main axis about 1.5 mm wide. Internode up to 19 mm long, shortening distally. The proximal oval body 1–1.8 mm in diameter. Apical projection 1.6–2.6 mm long, 48–120 μm wide.

Description: The part and counterpart, red in color, of the same distal portion of plant are preserved as compression, embedded in slightly yellowish siltstone (Fig. 2a). All appendages are physically connected to a common axis (Fig. 2a). The axis is slender and straight, about 50 mm long and 1.5 mm wide, with longitudinal ridges (Fig. 2a, c). There are distinct joints and internodes (Fig. 2a). The internode is up to 19 mm long, shortening distally (Fig. 2a). Bracts are strap-like, about 8 mm long and 1.1 mm wide, oppositely arranged along the axis (Fig. 2a, d). A female part is up to 8 mm long and 5 mm wide, axillary, either sessile (Fig. 2c) or on a pedicel up to 13 mm long (lower arrow in Fig. 2a), becoming smaller distally (Fig. 2a). Female parts have lanceolate scales surrounding their central units (Figs. 2a, c, 4a–e). The scales are about 4 mm long and 0.7 mm wide (Fig. 2c). The central units are surrounded by two envelopes (Figs. 2c, f, h, 3a, e). The outer envelope is up to 3.5–4 mm long, 0.75 mm thick at the distal, with ground tissue of isodiametric cells about 20 μm in diameter (Figs. 2b, c, f, h, 3a–c, e). The inner envelope surrounds the central unit, crateriform, 0.76 mm above the oval body, and buttresses only the proximal portion of the apical projection (Figs. 2b, c, f, h, 3a, e). The oval body is 1–1.8 mm in diameter, solid, surrounded by a wall about 117 μm thick, separated from the inner envelope (Fig. 2b, c, f, h). The apical projection protrudes through both envelopes, and is cylindrical, solid, straight or slightly curved, up to 2 mm long and 83 μm in diameter, including epidermis and ground tissue inside, either preserved as a solid cylinder raised above the sediment matrix or leaving a groove on the sediment when missing (Figs. 2c, f–j, 3a–g). The ground tissue in the apical projection is of isodiametric cells 18–19 μm in diameter (Fig. 3b–d, f, g). The terminus of the apical projection appears truncated (Fig. 2j).

Etymology: *paradoxa*- for the mysterious affinity of the fossil.

Holotype: NOCC201204261301 (Fig. 2a).

Paratype: NOCC201204261302.

Depository: The National Orchid Conservation Center of China, Shenzhen, China (NOCC).

Remarks: Both the distal (apical projection) and proximal (oval body) parts of the central unit are bulging above the sediment surface when preserved or leaving depressions on the sediment when missing. Their three dimensional configurations constitute a strong contrast against the axis, which demonstrates less bulging form. This contrast implies that the central unit is more robust than the axis in *Pseudoephedra*.

The general configuration of the female parts varies from the bottom to the top of the fossil. For example, the pedicel is obvious in the basalmost pairs of female parts but almost nonexisting in the topmost pair (Fig. 2a–c). This difference can be attributed to the maturity and development of the organs.

4. Discussions

The oval body of the central unit is situated in the center of the female part in *Pseudoephedra*. The homology of this oval body is hinged with the affinity of *Pseudoephedra*, for which the vegetative features are helpless in this special case. Given its huge size, position, and morphology, male part is apparently out of the question, and the oval body in *Pseudoephedra* could only be plausibly interpreted either as (1) a nucellus with a long beak, (2) an ovule with a micropylar tube, or (3) an ovary with a style. We will discuss each alternative, its implications and credibility below.

4.1. First alternative

A nucellus with an apical beak is not rare among gymnosperm taxa. The Devonian proto-ovule *Runcaria* has a distal projection similar to that of *Pseudoephedra* (Gerrienne and Meyer-Berthaud, 2007). Given that the relationship between *Runcaria* and later evolved seeds is still mysterious, that it is from the Devonian, and that its vegetative parts are unknown, comparing Cretaceous *Pseudoephedra* including various organs with *Runcaria* is very premature. In *Cycas* and *Zamia*, the nucellus has its beak exserted above the integument and is exposed to the exterior (Zhang, 2013). If this nucellar beak became more elongated, then a solid apical projection just like that of *Pseudoephedra* would come into form. But relative length of these beaks in cycads is too short to be comparable with those in *Pseudoephedra*. Furthermore, two envelopes surrounding the apical projection, branching pattern, and general morphology are characters sufficient to distinguish *Pseudoephedra* from any cycads. Nucellar beaks of various morphologies are frequently seen in gymnosperms (e.g., *Stephanospermum*, *Feruglioclad*us, *Otovicia*) (Archangelsky and Cuneo, 1987; Drinnan et al., 1990; Kerp et al., 1990; Spencer et al., 2013) and may be routine structure

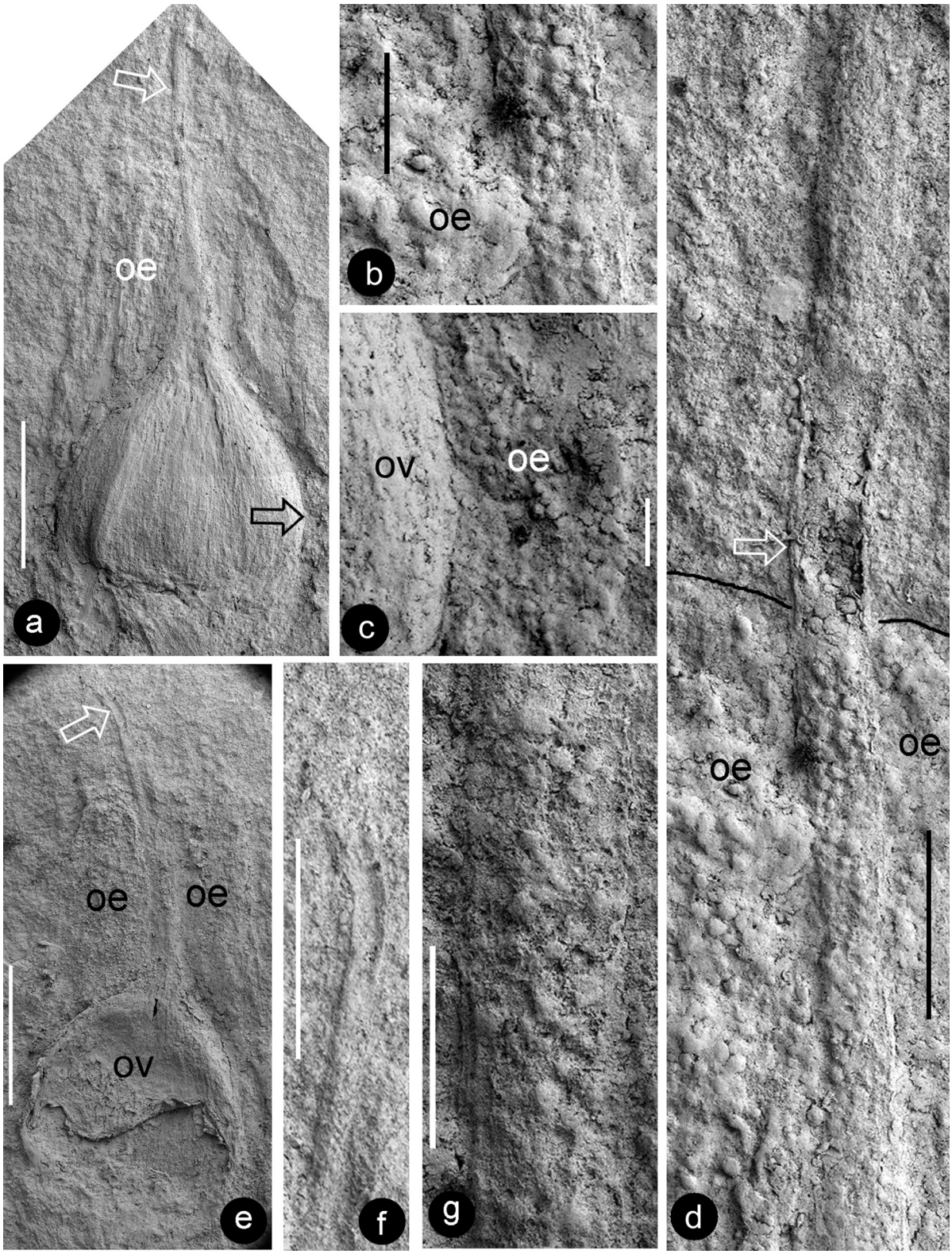

Fig. 3. Details of *Pseudoephedra paradoxa* n. gen. n. sp. SEM. (a) Replica of the female part shown in Fig. 2f, showing the inner envelope and outer envelope (oe) surrounding the oval body and its apical projection (white arrow); scale bar = 1 mm. (b) Detailed view of the granular ground tissue of isodiametric cells in the apical projection (right) and outer envelope (oe, left), enlarged from (a) and (d); scale bar = 0.1 mm. (c) Detailed view of the granular ground tissue of isodiametric cells in the outer envelope (oe, right) adjacent to the oval body (ov), enlarged from the region marked by black arrow in (a); scale bar = 0.1 mm. (d) The apical projection shown in (a); note the epidermis (arrow) and ground tissue in the apical projection and outer envelope (oe); fracturing at different levels reveals various inner and surface details of the long apical projection; scale bar = 0.1 mm. (e) Replica of the female part shown in Fig. 2h, with oval body (ov) and its apical projection (arrow) surrounded by inner envelope and outer envelope (oe); scale bar = 1 mm. (f) The apical projection shown in (e); scale bar = 0.5 mm. (g) Granular ground tissue of isodiametric cells in the apical projection shown in (f); scale bar = 0.1 mm.

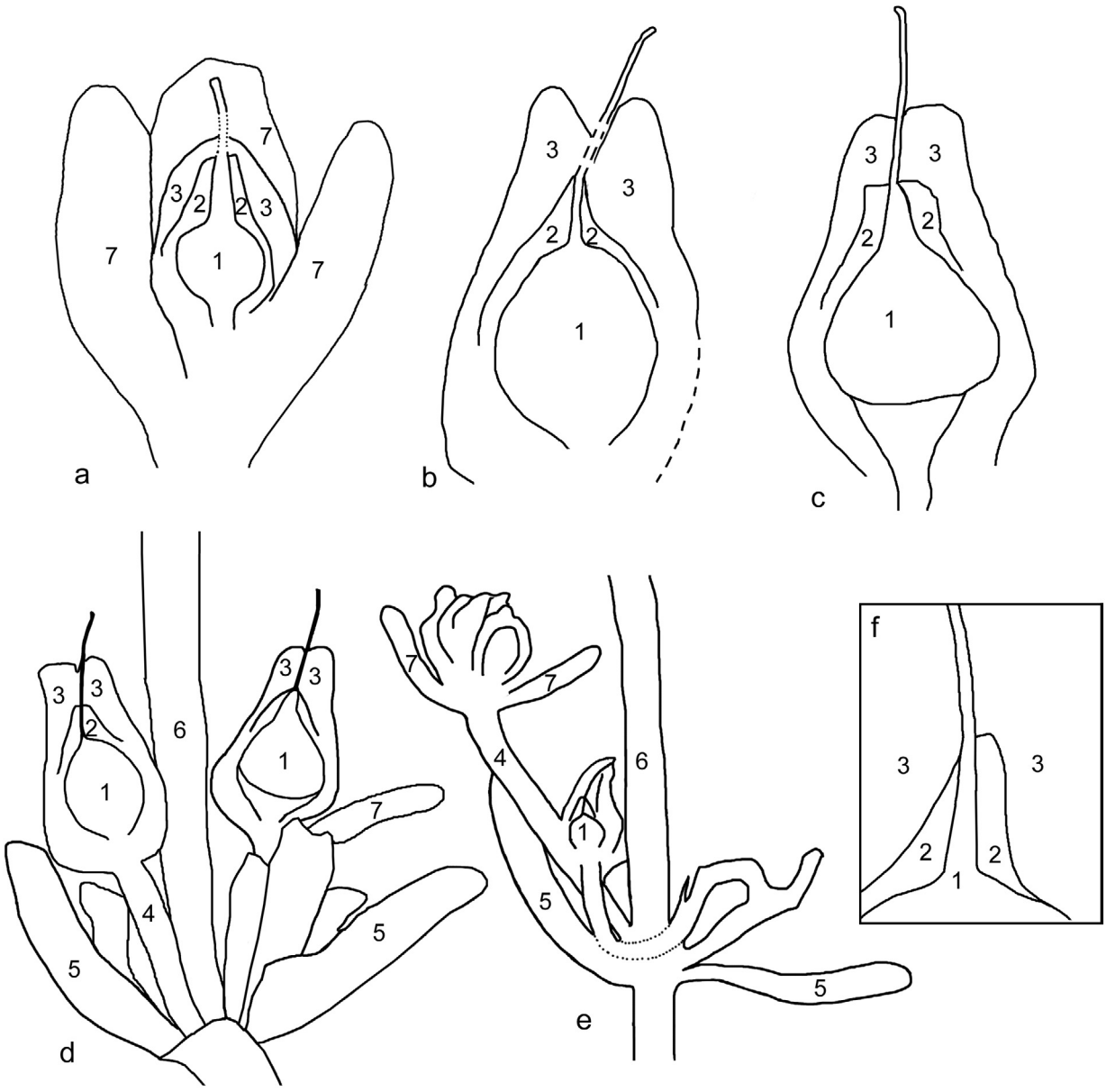

Fig. 4. Sketches of *Pseudoephedra paradoxa* n. gen. n. sp., showing details of female parts. Labels for all: 1, oval body; 2, inner envelope; 3, outer envelope; 4, pedicel; 5, bract; 6, axis; 7 scale. (a) The immature female part in Fig. 2b, showing the central unit surrounded by two envelopes. (b) Female part marked by 3 in Fig. 2a, showing the central unit surrounded by two envelopes. (c) Female part marked by 2 in Fig. 2a, showing the central unit surrounded by two envelopes. (d) The pair of female parts arrowed by the upper arrow in Fig. 2a oppositely arranged in axils of subtending bracts. (e) The lowermost pair of female parts in Fig. 2a oppositely arranged in axils of subtending bracts; note the elongated pedicels and one of them bending to the opposite side. (f) Sketch of Fig. 2e, showing two envelopes surrounding the oval body and its apical projection.

for many. But these nucellar beaks are very short and always hidden in the micropyles, and must play a role in pollination quite different from that in *Pseudoephedra*. And lack of information on other parts of these gymnosperms makes our further comparison impossible and unnecessary. A typical nucellus does not have a separable wall around, this generalization conflicts with the presence of a thin wall around the oval body in *Pseudoephedra* (Fig. 2k), therefore nucellus is apparently not an ideal candidate in this case. All considered, the distal projection of *Pseudoephedra* has little to do with the nucellar beaks seen in gymnosperms, and the oval body of *Pseudoephedra* cannot be a counterpart of nucellus, either.

4.2. Second alternative

If the oval body with distal projection in *Pseudoephedra* were compared to an ovule with micropylar tube, then the female part of *Pseudoephedra* would be very similar to that of *Ephedra*, namely, an ovule surrounded by envelopes. This comparison appears as if further strengthened if the general morphology of *Pseudoephedra* is taken into consideration. *Pseudoephedra* demonstrates a great resemblance to *Ephedra* (Ephedraceae) in dioecy, growth habit, opposite branching pattern, obvious joints and internodes, envelopes free from the nucellus except at the base, obvious apical projection (Chamberlain, 1957;

Bierhorst, 1971; Martens, 1971; Rydin et al., 2010; Rothwell and Stockey, 2013) (Table 1). These characters shared between *Pseudoephedra* and *Ephedra* suggest that *Pseudoephedra* appears to fall well into the scope of the Ephedraceae. This comfortable-appearing placement remains plausible until detailed information of the apical projection is taken into consideration. We recognize the solid nature of the apical projection in *Pseudoephedra* because other alternatives can be easily eliminated. One alternative is that the apical projection is simply a micropylar tube that is filled up with pollen grains or sugar/starch. This pollen-grain-interpretation might sound plausible considering the size of the granules in the apical projection (about 20 μm in diameter, Fig. 3b–d, f, g) perfectly matches that of pollen grains. However, this alternative appears absurd when the granules of similar morphology are also seen in the outer envelope of *Pseudoephedra* where pollen grains are not expected (Fig. 3c). In addition, there is no report of micropylar tubes completely filled up with pollen grains yet. Sugar or starch is present in pollination drop of Gnetales, but such sugar/starch, if preserved, should be amorphous and shrunken rather than granular and micropylar-tube-full-filling, and they should not be seen in the outer envelope, either. Therefore we have to drop this alternative. Another alternative is that micropylar tube in *Pseudoephedra* is blocked after pollination, as in Gnetales and Erdtmanithecales (Friis et al., 2007; Rothwell and Stockey, 2013). However, the blocking of micropylar tube in Gnetales and Erdtmanithecales is restricted to the segment bracketed by the outer envelope and micropylar tube remains open apically (Friis et al., 2007, 2011). The "blocking" in *Pseudoephedra* is seen in the whole length of the apical projection and well above the assumed outer envelope (Fig. 3b, d, f, g), thus distinct from the cases in Gnetales and Erdtmanithecales. Three dimensionally preserved apical projection of *Pseudoephedra* shows no trace of tubular structure: it shows little deformation in spite of the pressure from the overlying strata, which, in contrast, has heavily compressed the axis of the same fossil. When missing, the apical projection of *Pseudoephedra* leaves a groove on the sediment; when preserved, it is preserved as a cylinder bulging above the sediment (Figs. 2f–j, 3b–d, f, g), implying that the apical projection of *Pseudoephedra* is a solid rather than tubular structure. This single character prevents us from placing *Pseudoephedra* safely in Ephedraceae.

Apparently, forcing *Pseudoephedra* into the Ephedraceae (Gnetales) would incur many troubles for botanists. On one hand, the solid apical projection implies angio-ovuly in *Pseudoephedra*. If it were placed in Ephedraceae, it would mean that the ovules have no chance to be exposed at pollination in Ephedraceae and they would have to adopt the pollination mode typical of angiosperms. This treatment would destroy the last distinction between angiosperms and Gnetales (especially *Gnetum*, which is hard to be distinguished from eudicots in all but one aspects). On the other hand, the BEG group (Bennettitales, Erdtmanithecales, and Gnetales) has only one synapomorphy, micropylar tube (Friis et al., 2007, 2009). Lumping *Pseudoephedra* without micropylar tube into Ephedraceae (Gnetales, BEG clade) would destroy the only synapomorphy of whole BEG clade. This would cast further doubt over the validity of BEG clade, in addition to those raised by others (Rothwell

Table 1
Comparison among *Pseudoephedra*, *Ephedra*, and other more or less related taxa.

	Pseudoephedra	*Ephedra*	*Anabasis*	*Stephanospermum*	*Cycas*, *Zamia*	Feruglioladaceae	*Otovicia*	*Runcaria*
Habit	Shrub?	Shrub	Shrub	?	Woody	Woody	Woody	?
Phyllotaxy	Opposite	Decussate	Decussate	?	Helical	Helical	Helical	?
Joint and internode	Yes	Yes	Yes	No	No	No	No	No
Number of envelopes	2	2	0	1	1	1	1	1
Ovulate unit	Axillary	Axillary	Axillary	Stalked	Non-axillary	Axillary	Axillary	Stalked
Sexuality	Dioecious	Dioecious, rarely monoecious	Monoecious	Dioecious	Dioecious	Dioecious	Dioecious	Dioecious
Apical projection	Solid, long, emergent	Tubular, long, emergent	Solid, long, emergent	Solid, short, hidden	Solid, short, emergent	Tubular, short, hidden	Funnel-like, short, hidden	Solid, long, emergent
Age	Cretaceous	Cretaceous–Extant	Extant	Carboniferous	Extant	Permian	Carboniferous–Permian	Devonian
Reference		(Biswas and Johri, 1997; Wang and Zheng, 2010)	(v. 5 of Wu et al., 2013)	(Drinnan et al., 1990; Spencer et al., 2013)	(Zhang, 2013)	(Archangelsky and Cuneo, 1987)	(Kerp et al., 1990)	(Gerrienne and Meyer-Berthaud, 2007)

et al., 2009; Tekleva and Krassilov, 2009). Considering all, we think that it is not wise to place *Pseudoephedra* in Gnetales.

4.3. Third alternative

If the oval body with distal projection in *Pseudoephedra* were taken as an ovary with a style, then the female part of *Pseudoephedra* would be equivalent to female flower of angiosperm. The scales surrounding the female part would be interpreted as perianth elements, the apical projection the style, and the whole fossil an inflorescence. This interpretation is strongly favored by the solid nature of the apical projection and thin wall around the oval body of *Pseudoephedra* (Figs. 2a–c, e–k, 4a–d, f). The solid nature of the apical projection makes gymnospermous pollination an impossibility. Different pollination modes have been used to distinguish angiosperms and gymnosperms for more than a century (Arber and Parkin, 1907; Martens, 1971; Cronquist, 1988; Biswas and Johri, 1997; Tomlinson and Takaso, 2002): the ovules in Gnetales are pollinated by pollen grains drained in through the micropylar tube, whereas those in angiosperms are typically pollinated by sperms transported through pollen tubes that penetrate style tissues. The famous Mesozoic plant *Caytonia* had once been put in angiosperms due to its enclosed seeds (Thomas, 1925) but later transferred into gymnosperms due to the presence of pollen grains in the cupules (Harris, 1933). Parallel to this, *Gnetum* appears like a perfect eudicot but it is rationally placed in gymnosperms because of its pollination mode. Both of these examples, fossil and extant, convincingly demonstrate that complete enclosure of ovules before pollination ensures an angiosperm affinity for a plant. Although talking about pollination of *Pseudoephedra* appears very speculative at this time, the solid nature of the apical projection in *Pseudoephedra* makes it hard to conceive that pollen grains could enter the oval body. The thin wall around the oval body (Fig. 2k) strengthens that the oval body is actually is ovary, and the thin wall is the ovarian wall that completely secludes the interior space, suggestive of angiospermy. Thus placing *Pseudoephedra* in angiosperms is a rational choice. The challenges for this interpretation include *Ephedra*-like morphology and two surrounding envelopes of *Pseudoephedra*. However, this is not the first time to see *Ephedra*-like angiosperms. For example, *Anabasis* (Amaranthaceae) is a eudicot that is hardly distinguishable from *Ephedra*, and Early Cretaceous *Chaoyangia* was frequently placed in Gnetales due to its *Ephedra*-like decussate branching pattern alone (Sun et al., 1998) although detailed studies indicate that *Chaoyangia* is a monoecious angiosperm (Duan, 1998; Wang, 2010). Two envelopes surrounding an ovary is rare but not unseen in angiosperms, for example, the ovary with distal style in Fagaceae and Juglandaceae (Bhattacharyya and Johri, 1998) is surrounded by additional layers. Thus it seems not a problem placing *Pseudoephedra* in angiosperms, although this treatment would make the boundary between angiosperms and gymnosperms vague or disappearing, just as Darwinism expects.

Despite all, we wish to be conservative now, treat *Pseudoephedra* as *incertae sedis* for the time being, and wait for more investigations to shed new light on the affinity of *Pseudoephedra* in the coming years.

5. Conclusions

Pseudoephedra is an enigmatic Early Cretaceous plant that demonstrates a great resemblance to Ephedraceae. But, instead of having micropylar tube (characteristic feature of Gnetales), *Pseudoephedra* has a solid apical projection, which resembles styles in angiosperms. Placing *Pseudoephedra* in any known group of gymnosperms is premature in the current knowledge context.

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